



A WEEKLY ILLUSTRATED JOURNAL OF SCIENCE.

"To the solid ground
Of Nature trusts the mind which builds for aye."—WORDSWORTH.

THURSDAY, NOVEMBER 5, 1908.

ALTERNATION OF GENERATIONS IN PLANTS.

The Origin of a Land Flora. A Theory based upon the Facts of Alternation. By Prof. F. O. Bower, F.R.S. Pp. xii+727; with numerous illustrations. (London: Macmillan and Co., Ltd., 1908.) Price 17s. net.

THIS important book, embodying the results of the author's well-known morphological researches during the last twenty years, may be regarded from two points of view. On the one hand, it forms a most excellent manual of comparative morphology for the groups dealt with—essentially the higher cryptogams; on the other, it gives the final statement of those theoretical views on the alternation of generations in plants with which Prof. Bower's name is associated and of which he is the leading champion. The two aspects cannot, however, be kept separate; the theory forms the thread on which the facts are strung, and without the theory we should not have had those researches which have so greatly enlarged our knowledge of the facts. In this way the "working hypothesis" has fully justified its existence, and all botanists owe a debt of gratitude to the author for the theory which he has so systematically worked out, as well as for the detailed investigations to which it has been the guide. No more important contribution to scientific botany has appeared in England since the revival of botanical research in this country in the 'seventies of the past century.

It is needless to say that the author's presentation of the facts is everywhere scrupulously fair; his book may be used with profit and pleasure alike by those who accept and those who dissent from his main position. The reviewer cordially agrees with the concluding sentence of the preface:—

"Whatever view be ultimately taken of the prime origin of the alternating generations, many of the conclusions arrived at here as to the morphological progress and phyletic grouping of the Archegoniata

will stand: they have a validity of their own quite apart from any question of the ultimate origin of the sporophyte, which has finally become the dominant factor in the flora of the land."

The book is divided into three parts:—Part i., statement of the working hypothesis, 20 chapters, 254 pp.; part ii., detailed statement of facts, 20 chapters, 402 pp.; part iii., conclusion, 7 chapters, 60 pp.

This arrangement involves a certain amount of repetition, but, on the whole, is well adapted to the purpose of the book, which is to state the main theory with its subsidiary hypotheses, and to test them fully in their application to the morphological data.

In considering the book critically, attention will be chiefly directed to its theoretical side. The reviewer is one of those who are unable to accept the chief conclusions of the author, and hence it is impossible altogether to avoid controversy. From what has already been said, it will be clear that theoretical differences in no way affect the high estimate of the value of Prof. Bower's book which every unbiased reader must form.

After an introductory chapter on the scope and limitations of comparative morphology, the life-history of a fern is appropriately given the foremost place as the type of the regular alternation of sexual and asexual generations which characterises the higher plants. In the ferns and the vascular plants generally the asexual generation is the plant itself, with all its elaboration of vegetative organs, while the sexual phase is represented by the comparatively small and simple prothallus. In the Bryophyta (mosses and liverworts), on the other hand, the balance of the two generations is reversed, the main vegetative development falling in the sexual stage, while the asexual generation is merely a fruit (sporogonium) dependent throughout life on the sexual plant which bears it. In both classes "there is thus a marked difference between these two phases, and their sequence may be said to constitute an *antithetic alternation*" (p. 32). Here, and in some other passages (e.g. p. 658), the phrase "antithetic alternation" is used simply to express the known facts

of the life-history; elsewhere, however (as on p. 159), the words are employed in a different sense, namely to indicate the author's theory that the asexual generation has been intercalated in the life-cycle, and is therefore newer than the sexual phase or gametophyte. To avoid confusion it will be best to speak of this view as the "intercalation theory," though the term "antithetic" has come to be identified with it. The significance of the title, "The Origin of a Land Flora," lies in the fact that the sexual generation retains, at least throughout the archegoniate cryptogams, the primitive method of fertilisation by spermatozooids, requiring the presence of water, while on the other hand the asexual phase, with its wind-scattered spores, is essentially adapted to a terrestrial life. Hence the author speaks of the alternation as "amphibious," an appropriate phrase which may be readily adopted, whatever view be taken of the origin of the two generations. The asexual sporophyte, however it may have arisen, conquered the dry land; the gametophyte, with its conservative adherence to traditional methods, remained dependent on a more or less watery environment, until the seed-plants came to be evolved. Then the prothallus became a mere parasite on the sporophyte, enclosed within the megasporangium, so that fertilisation could take place on the plant itself. Spermatozooids were retained in the more primitive types (cycads, Ginkgo, and no doubt many fossil seed-plants), but their swimming was now confined to a water-drop secreted within the ovule; in the rest of the Spermatophyta they have dropped their now useless motility, and fertilisation, like the other vital processes, has become thoroughly adapted to terrestrial conditions.

All this is admirably told in Prof. Bower's book; and it is to him that the credit belongs of realising the essential biological significance of alternation of generations as it exists in the higher cryptogams.

The question at issue relates to the origin of the alternating generations. On the intercalation hypothesis, maintained by Prof. Bower in agreement with Celakovsky and some other morphologists, the sexual generation represents the original plant, which alone existed in the presumed ancestor, while the asexual sporophyte is a new development, an intercalation, arising from the elaboration of the fertilised ovum or zygote, first into a mass of spores, and ultimately into a complex sporogonium on the one hand or a spore-bearing plant on the other.

The strength of the intercalation theory lies in the evidence afforded by certain liverworts (Ricciaceæ), in which the sporogonium actually consists of nothing but a spherical mass of spore-mother-cells, enclosed in an ephemeral epidermis. So simple a body might well have arisen as a new formation, as a fruit-body replacing an oospore, a development for which various apparent analogies have been traced among thallophytes. From the Ricciaceæ there are found sufficiently continuous series of forms, leading up to the fully differentiated capsules of the higher liverworts and the mosses. Hence the intercalation theory appears quite credible for the Bryophyta, and some botanists have accepted it for that class while rejecting it for the Pteridophyta.

NO. 2036, VOL. 79]

Even as regards the Bryophyta, however, everything depends on the primitive nature of the Ricciaeous sporogonium, and this is open to doubt. As the author himself says (p. 237):—"It may be a question whether the absence of a nutritive system is due here to reduction, or is itself the primitive state." Though "the latter is the view usually accepted," there is good evidence for reduction in related liverworts (*Cyathodium*, pp. 237 and 263), and in *Riccia* itself the transitory nature of the sporogonial wall (p. 257) may well indicate a secondary loss or change of function, as we see in the case of the nucellus of so many angiospermous ovules. There are good grounds for holding that far-reaching reduction has gone on even among the higher Bryophyta, and, on the whole of the evidence, the idea of ascending series within this class, starting from the simplest form of sporogonium, cannot be considered as by any means established. In fact, the Bryophyta, which have long been regarded as affording the clue to the interpretation of the life-cycle of the higher plants, themselves stand in need of interpretation, even more than other groups.

Among the Vasculares, the sporophyte is always (even in *Lycopodium Selago*!) a highly organised plant, and no one would dream of attributing its origin to an intercalation, if it were not for the analogy of the bryophytes.

During the last fifteen years the cytological distinction between the two generations has played an important part in the controversy as to their nature. In all normal cases the asexual generation is "diploid," its nuclei having twice as many chromosomes as those of the "haploid" sexual phase. Reduction takes place in the spore-mother-cell, at the initiation of the gametophyte. This side of the subject is very ably treated by Prof. Bower, who continues to attach considerable importance to the cytological distinction, in spite of the exceptional cases recently brought to light, where it has been shown with certainty that the gametophyte generation may be diploid, and, with great probability, that the sporophyte may be haploid. Such cases are associated with the occurrence of apospory (suppression of spore-formation) and apogamy (suppression of sexual reproduction) in the same life-cycle, as happens in various anomalous ferns. These observations prove that there is no necessary connection between the number of chromosomes and the morphological characters of the alternating generations, but "cannot be held to invalidate the view that the cycle as above stated existed in all probability throughout the earlier phases of descent of the Archegoniata" (p. 62).

The cytological distinction was at one time regarded as supporting the opinion that the two generations were distinct in origin, and thus as favouring the intercalation theory. This can no longer be maintained, since it has been shown by Lloyd Williams and Mottier that in the alga *Dictyota* there is a regular alternation between the haploid sexual and the diploid asexual generation, generations which in all morphological respects are perfectly similar to one another. There can be no question of intercalation

here, and the case of Dictyota (as well as the more complex case of certain Florideæ) shows that the cytological distinction may exist between generations which are clearly homologous with one another. The author explains the similarity of the two generations in such cases by the similarity of the conditions to which they are exposed (p. 81). We can well understand (though this is not the author's view) how, when the conditions became different, as in the Archegoniatae, generations likewise homologous may have come to be sharply differentiated. The author, in chapter v., gives an admirable account of the facts, but perhaps hardly realises how unfavourable they are to the theory of intercalation.

There appears to be no satisfactory case among the Thallophyta of the origin of a diploid asexual phase by intercalation, unless it be among certain fungi, too remote from the archegoniate series to afford any serviceable analogies.

The fruit-body of the green alga *Coleochæte*, formerly regarded as comparable to a simple bryophytic sporogonium, has been shown by Allen to have haploid structure, reduction taking place on the first nuclear division in the germinating zygote (p. 73). Hence this time-honoured comparison will no longer hold good, though some biological analogy may still be traced.

So far as the evidence from the Thallophyta is concerned, it seems that recent work favours the origin of the alternating generations by the modification of homologous individuals rather than by the intercalation of an entirely new phase in the life-cycle.

Those morphologists who maintain the intercalation hypothesis differ among themselves as to the relation between the leafy sporophyte of the higher plants and the sporogonium from which they believe it to have been evolved. To some, the leaf is the primary structure, derived directly from the sporogonial head, and the axis is entirely subsidiary (Cela-kovsky and Worsdell), while on Prof. Bower's view the axis is primary, the leaves (sporophylls) arise from it *de novo*, by "enation," and the roots are likewise accessory. The author lays great stress on the predominance of the axis, as the foundation of his "strobiloid" theory, according to which the whole plant represents an elaborated strobilus, which in its turn was derived from a simple sporogonium-like fructification. He supports his view by a wealth of argument, based on anatomy, embryology, and comparative morphology (see especially chapter xi., the theory of the strobilus). All this, however, is subsidiary to the main question. The predominance of the axis is no necessary part of the "antithetic theory," nor is it in any way opposed to the homology of the sporophyte with the vegetative body of the lower plants. We see quite clearly among the Bryophyta how, starting from a thalloid structure, the axis may become predominant, and analogies are not wanting among the Thallophyta also.

We will not, however, pursue these controversial matters further. Prof. Bower deals in the fullest manner with a great problem, and nothing could be better than the way in which he states his case. He is not, perhaps, quite so happy in his treatment of

alternative hypotheses, which he sometimes dismisses rather curtly, though to many botanists they will appear worthy of more serious consideration. The question, as the author points out, scarcely admits of any final solution. The gaps in the evidence are such that no theory (least of all the author's) can dispense with the postulation of "hypothetical organisms," nor have we much reason to hope that the fossil record will ever supply a more substantial ancestry.

The second and longest division of the book, the detailed statement of the facts, will probably prove of most value to the student, for it gives a full account of the morphology, anatomy, and embryology of the sporophyte of the Archegoniatae (including extinct groups), with incidental references to the other generation. Here also the strobiloid theory permeates the whole, and great importance is attributed to the *Lycopodium Selago* type, as the best living representative of the hypothetical "strobiloid condition" in which all the leaves were sporophylls. A figure of this species forms the frontispiece to the book.

The Sphenophyllales (including Psilotaceæ) and Equisetales are appropriately grouped together under the head of "Sporangiophoric Pteridophyta," characterised by the sporangia being borne on definite outgrowths from the axis or leaf, the peltate scales of an *Equisetum* affording the most familiar example. The author maintains at length the view that the sporangiophore is an organ *sui generis*, not homologous with a leaf or leaf-lobe, a position which is tenable and simple, but not wholly convincing to those whose point of view is different from that of the strobiloid theory.

The Ophioglossaceæ are treated in much detail; the author upholds his well-known opinion that this family forms, as a whole, an ascending series, probably derived from some sporangiophoric type comparable to that of the Psilotaceæ or other Sphenophyllales. He thus makes the series a parallel development to the ferns, without actual affinity with them. The alternative, and, in the reviewer's opinion, more probable view, that the Ophioglossaceæ are derived from a somewhat primitive group of ferns, not very remote from the Botryopterideæ, is not discussed. The author argues vigorously against saprophytic reduction as a factor of any importance in the evolution of this family, though in his description of *Ophioglossum simplex* he has himself supplied the most convincing proof that such reduction has occurred in an extreme degree. The extraordinary embryology of the genus *Ophioglossum* (the embryo in some species consisting of a root and nothing else) appears to indicate that we are here dealing with very highly modified plants, and by no means with types of primitive simplicity.

The account of the ferns is extremely full and interesting, and less influenced by theoretical considerations than the rest of the book. The author's classification of the homosporous ferns according to the arrangement and succession of development of their sporangia was first published in 1899, and has been recognised as a convenient and natural grouping. The three series are characterised as follows (p. 497):—

The Simplicies, in which the sporangia of a sorus

are produced simultaneously; the *Gradatæ*, in which there is a definite succession in time and space; and the *Mixtæ*, in which there is a succession in time, but no regular succession in space.

"These three types appeared successively in geological time: the *Simplices* were the characteristic ferns of the primary rocks, though many of that type still survive; the *Mixtæ* are the dominant ferns of the present day, while the *Gradatæ* take a middle place."

The scheme on p. 653, showing the approximate relations of the several families of ferns, will be of great service to students of this class (now more important than ever to the morphologist). Altogether, the author's account of the *Filicales* is no doubt the best yet published.

The concluding part of the book gives a full and final statement of the author's theoretical position, and is the part which will most appeal to the reader whose interest lies mainly in the theory rather than the details. Enough, however, has been said on the points in dispute; any attempt at a full discussion would far exceed the limits of a review.

The book is excellently got up, with abundant and admirable illustrations throughout. It is almost free from misprints. One, however, occurs in an important passage on p. 237, where "*Riccia* cell" appears to be a printer's error for "*Ricciaceæ*."

Nothing can be better for English botany than the appearance of such a book as this, a full and most original treatise on an important branch of the science by one who is an acknowledged master of his subject. Prof. Bower is to be warmly congratulated on this, the latest product of his energy and devotion to research.

D. H. S.

WINDMILLS AND WATER-WHEELS.

Natural Sources of Power. By R. S. Ball. Pp. xvi+348. (London: A. Constable and Co., Ltd., 1908.) Price 6s. net.

THE classification of a source of power as a "natural" one is purely arbitrary. The distinction would imply that a source of power could be "artificial," which would, of course, contradict the first law of thermodynamics. The author of the present volume simply uses the word to describe those sources of power which provide us directly with mechanical energy without any intermediate transformation, such as combustion or the like; and the two particular supplies of energy to which attention is directed are wind-power and water-power.

As is natural, the author commences his book with a reference to the, said to be, not distant day when all the coal, and all the oil, in the world will have been used up, and mankind, in order to sustain itself, will have to rely wholly upon the water-wheel and the windmill for that tremendous amount of energy which will be necessary to keep the immense population of the earth in the state of comfort to which it has, with the progress of civilisation, attained. It is an interesting speculation to picture to oneself what the state of the world will be when this prophesied day arrives, and the coal-measures of the world have

disappeared. Will the great manufactures migrate from Lancashire and Northumberland to Norway, Italy, and the West of Ireland, or will, ere that day arrives, our cotton mills and blast furnaces be run by radium engines, utilising sources of energy which are at present wholly unexploited? Certainly, nobody who has studied the development within the last few years of the science of radio-activity will be prepared, out of hand, to deny the possibility.

It is rather surprising to be told that the demand for windmills was never so great as it is to-day, or the trade of the manufacturer of such motors never so brisk. On the other hand, evidences of the utilisation of the water-powers of the world are everywhere abundant, the chief agent in this being the development of electrical technology. A book, therefore, such as the one under review, dealing with these subjects in an easily understandable manner, is to be accorded a welcome. The style of the book, while being simple, is yet not entirely popular. It is not a complete treatise, a certain amount of elementary mathematics is necessary, but the calculus is not used, the author giving a general review of his subject, with the object of showing the desirability of not allowing the many small sources of wind- and water-power which exist to run to waste. The book can be specially recommended to those readers who, while not being specialists in the particular branch dealt with, desire to obtain a general survey of the subject.

The first chapter deals with general principles, such as the distinction between "power" and "energy," efficiency of machines, units, &c. The discussion of the electrical units of energy on p. 7 is hardly happy. This, we think, is due to the author placing in juxtaposition the "foot-pound" and the "watt," which latter, he says, is "allied to a power unit." The confusion in electrical units of power, which the author mentions, is, we think, entirely of his own creation. The watt is not "allied" to a power unit, but is actually the electrical unit of power, there being really no confusion in the matter at all.

Chapter ii. is concerned with "water power and methods of measuring." As is only fit, the fundamental theorem of Bernoulli, which says that the sum of the pressure head, the velocity head, and the height above datum level is the same at all points in a pipe running full of water, is stated and discussed, as are also weirs and the general principles of surveying as called for in the lay-out of a water development scheme.

Subsequent chapters deal with the different kinds of water-wheels and hydraulic turbines, their general design, theory and regulation. The construction of water-power plants and the fundamental principles of dams are also referred to, while descriptions of several typical installations working under such widely different conditions as heads of 2 feet and 2000 feet are given.

The last 120 pages of the volume discuss windmills and wind-motors. It is stated that there is a rapid extension and enormous trade done in small windmills. These are used chiefly in the great agricultural countries for pumping purposes, and the attempt made to utilise such motors for driving electrical generators